32. Scent Organs in Trichoptera. By Bruce F. Cummings, British Museum (Natural History) *.

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(Text-figures 1–8.)

Index.

Introduction.

Sericostoma personatum Spence is a tolerably common caddis-fly in Great Britain, and immediately attracts attention on account of the enormous development of the palpi of the first pair of maxillæ in the male. Unlike the maxillary palpi of the female, which are 5-jointed and quite normal (text-fig. 1), the maxillary palpi of the male consist of but a single segment very much enlarged and shaped like a half-moon. These two palpi are placed together and held vertically so as to mask the front of the head (text-fig. 2, p. 463).

Text-figure 1.

Sericostoma personatum.

Palpus of the first maxilla, ♀. × 17.

Despite their bizarre shape, these palpi have not obtained, so far as I am aware, that amount of enquiry into their nature and function which they deserve, and a résumé of their uneventful entomological history therefore will not detain us long.

i. Historical.

Kirby & Spence (1) regarded them as the genæ or cheeks of the skull. Pictet (2), as McLachlan gravely points out, "scarcely

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committed himself" to any direct statement as to the number of segments, though it seems more than likely, from an expression on p. 20 of his 'Recherches,' that he regarded three as probable. Stephens (3), p. 148, assumes two to be the number. Burmeister (4) says that according to his experience the segments of the maxillary palpi are only two in number. Rambur (5) agrees with this, and makes the observation regarding the "fluff" on the inner surface of the two palpi that it is perhaps not produced until some time after the insect has emerged, as all specimens do not possess it. Kolenati (6) arrives at the astonishing conclusion that there are four segments, the second being galeate and the third and fourth more slender. McLachlan (7) is cautious, and says "they are probably 3-jointed, but the basal joint is scarcely separable from the sides of the face and the second joint . . . . is ill-defined and transverse." A very brief and somewhat inaccurate description of the palpi follows. McLachlan's account appears to have set the matter at rest in the minds of Trichopterists, for Ulmer (8) in 1907 echoes the former's opinion that three segments are present, the first and second being ill-defined.

It is necessary to point out at once that, as will be seen on examination of text-fig. 2, McLachlan mistook the cardo and stipes of the first maxilla for segments of the palpi. A paper by W. Müller (9) in 1887 appears to have been overlooked, for here not only is the maxillary palpus described correctly as one-jointed, but convincing evidence is brought forward showing that these palpi serve as scent organs. Müller observed the large tuft of elongate hairs (McLachlan's inelegant but expressive "fluff") on the inner surface of the palpi and compared them with similar hair-tufts in the males of some Lepidoptera.

During copulation, one individual was seen "seine Palpen auseinander zu spreizen und die in denselben liegenden Haarbüschel zu entfalten," so that they surrounded the head "wie ein Heiligenschein." A strong smell of vanilla was emitted.

ii. Scent Organs in Insects.

By "scent organ" the entomologist usually means those glands which, secreting an attractive odour and being confined to the male sex, are supposed at mating time to charm or stimulate the females. Such scent glands, well known in the Lepidoptera, are situated at the bases of hairs arranged in tufts or at the bases of specially modified scales (called androconia) (10). Typical scent organs like these occur not only in the Lepidoptera (11) (12), but also in Coleoptera (*Blaps mortisaga*) (13), Blattidæ (15), and, as now appears, in Trichoptera (*Sericostoma personatum*).

Another type of scent gland occurs in insects. This assumes the form of fairly long eversible tubular filaments, usually two in number, and is known in the males of some Lepidoptera, *Spilosoma virginica*, *Arctia virgo*, *Haploë clymene* (10), and in the males of the Cricket, *Hadenœcus subterraneus* (17). Similar

retractile tubular filaments have not yet been described from the Trichoptera.

Under the term "scent glands" it is necessary also to include those hypothetical organs the emanation from which, in the females of certain moths, is supposed, in the well-known phenomenon of "assembling," to attract males from long distances. These *alluring* glands have not, I believe, been actually located, nor has the nature of such emanation been ascertained. Of course odoriferous glands undoubtedly do exist in many female Lepidoptera, and recently Ernst Urbahn (**21**) has made a detailed study of these glands, which are restricted to the abdomen and occur as intersegmental sacs, folds, and so on.

Then, again, in insects like the Musk Beetle (*Aromia moschata*), scent glands of still another type are found. These are pluricellular and open to the exterior by an aperture. In *Aromia* they are present in both sexes, though the aroma is stronger in the female, while the male is the more active organism.

It is often difficult to distinguish scent glands of this type from stink or repugnatorial glands used in self-defence. The resemblance is increased by the fact that some organs which have been described as stink glands, *e. g.*, in the Cockroach, *Phyllodromia germanica* (**16**), are nevertheless limited to the male. On the other hand, sac-like glands at the end of the abdomen of a Cricket, *Ceuthophilus maculatus* [(**10**) p. 393], occurring only in the male, are regarded as scent glands *.

There is, indeed, a widespread confusion in the literature of the subject, and it is difficult or impossible, in the present state of our knowledge of the natural history and mating habits of these insects, to say whether glands, occurring as they may in one sex only or in both, are of sexual import or are used in self-defence. *A priori*, stink glands if used in self-defence, one would expect to be either common to both sexes or, if limited to one sex, to occur in the female rather than the male †.

The occurrence of typical unicellular scent glands at the bases of hairs in Trichoptera as well as in Lepidoptera is interesting, and in view of the close relationship of these two Orders, not wholly unexpected. But in consequence of the common occurrence of scent glands in other insects besides Lepidoptera and Trichoptera, this cannot be taken in itself as evidence of phylogenetic affinity any more than can the presence of scales, which are also present in Trichoptera and Lepidoptera, but which occur also in Thysanura and other insects. Further, in *Sericostoma*, as will presently be shown, they occur on the

* The organs, called by their discoverer, Kraus, "duft organe" in *Aphlebia bivittata*, are named by Berlese "ghiandole repugnatorie."

† The stink gland, of course, must have been independently acquired very many times, for it is a device for self-defence adopted by many animals in very different phyla of the Animal Kingdom (*e. g.* Myriapods and Mammals). Scent or alluring glands are also common The mammalian anal, preputial, and inguinal glands are doubtless of sexual importance on account of their odoriferous secretions. Odoriferous glands occur also in crocodiles and snakes.

maxillary palpi, a position in which, I believe, they are unrecorded in the Lepidoptera.

Although Kellogg (18) has described and figured special plumules and scale-like hairs on the wings of Trichoptera, *e. g.*, *Mystacides punctata*, which function probably as androconia, scent organs have not, I think, been hitherto examined anatomically in this Order, for even in the paper in which Müller gives us an account of his discovery of the true function of the extraordinary palpi of *Sericostoma*, no account is included of the structure either of the palpi or of the glands.

In *Sericostoma* they differ in position from the scent glands of other insects. Scent glands are found on the abdomen or on the thoracic appendages. According to Berlese [(12) p. 525] odoriferous scales have been found on the palpi of some Saturnine butterflies, but he does not say whether they are the labial palpi or the maxillary palpi. Probably they are the former. Well-developed and characteristic scent organs occur in the labial palpi of an Indian butterfly, *Bertula chalybialis*; this, and the case of *Sericostoma personatum*, form the only well authenticated instances known to me of scent organs in the head, in the one case on the labial palpi and in the other on the maxillary palpi.

When not in use, the hair-tufts on the legs of the Lepidoptera with scent organs are often concealed in cavities, just as the hair-tuft of *Sericostoma* is concealed within the cavity of the inner surface of the maxillary palpi.

I anticipate that among the many strange modifications of the maxillary palpi of the males of many genera in the Family Sericostomatidæ, sometimes densely clothed with large black striated scales (*Gœra* and *Lepidostoma*), scent organs will be commonly found and their occurrence in the Trichoptera be very generally recognised.

It is evident that scent glands in insects are of fairly common occurrence and have been independently acquired over and over again. According to Berlese, hairs like androconia have been described from the wings of Diptera.

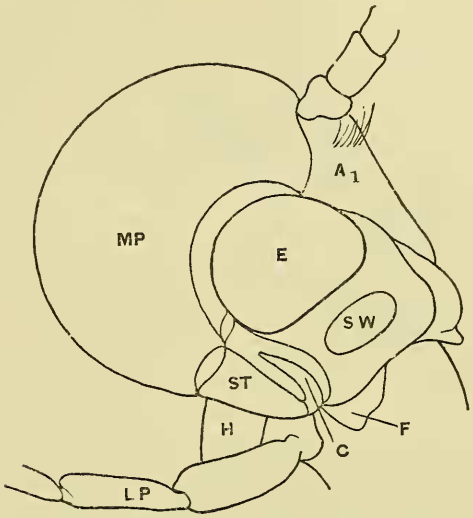
iii. The Maxillary Palpi of *Sericostoma personatum*.

Each palpus in outline is something like a half-moon. The outer surface is convex and strongly chitinous, dark brown in colour, with scattered short black hairs. The inner surfaces of the two palpi, which are carried closely apposed to each other, are concave, but their concavities are filled up to a level surface with an extremely thick felting of very long golden-yellow silky hairs. Until the palpi are separated with a needle the one from the other, the yellow felting lining the inner sides cannot be seen, or seen only with difficulty by looking at them edgeways from in front.

Both the palpi are held vertically with their broad surfaces facing

laterally (text-fig. 2). Together they entirely cover up the front of the head or clypeal region. Their tips are received each into a slot or excavation of the inner side of the enormously enlarged basal joints of the antennæ (text-figs. 4 & 5); emerging from underneath the palpi may be observed the tip of the white fleshy haustellum, the white tip of the labium and the lobes of the first maxillæ.

Text-figure 2.



Sericostoma personatum, ♂.

Head, side view (diagrammatic). × 22.

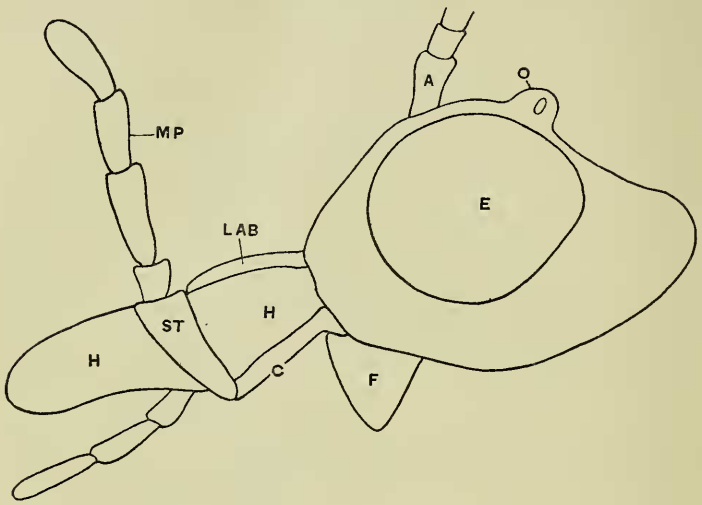
E. Eye. A_1. First segment of the antenna. *F.* Genal flap. *C.* Cardo. *ST.* Stipes. *H.* Haustellum. *MP.* Palpus of the first maxilla. *LP.* Palpus of the second maxilla. *SW.* Subocular wart.

In order to understand the modifications which have been drawn in the train of the enormous enlargement and porrection of the maxillary palpi, a few words are necessary upon the maxillary palpi and the structure of the head in other Trichoptera. In this Order, with the exception of *Plectrotarsus*, *Chimarrha*, and *Ptilocolepus* *, the lower side of the skull is incomplete, the gular region from the occipital foramen to the labium being soft and membranous. On either side the two

* The species examined were *Plectrotarsus gravenhorstii* Kolenati, *Chimarrha argentinea* Ulmer, and *Ptilocolepus granulatus* Pictet. *P. gravenhorstii* is the only species known belonging to its genus, and in the other genera it has been assumed that the observations following, recorded for the particular species, apply as well to the rest of the species of the genus.

genæ are drawn out ventrally into flaps, usually triangular in shape, which hang down as strong perpendicular walls beside the soft gular region (text-fig. 3, F).

Text-figure 3.



Phryganea, ♂.

Side view of the head (diagrammatic). Much enlarged.

E. Eye. *O.* Ocellus. *A.* Antenna. *F.* Genal flap. *C.* Cardo. *ST.* Stipes. *LAB.* Labrum. *H.* Haustellum. *MP.* Palpus of the first maxilla.

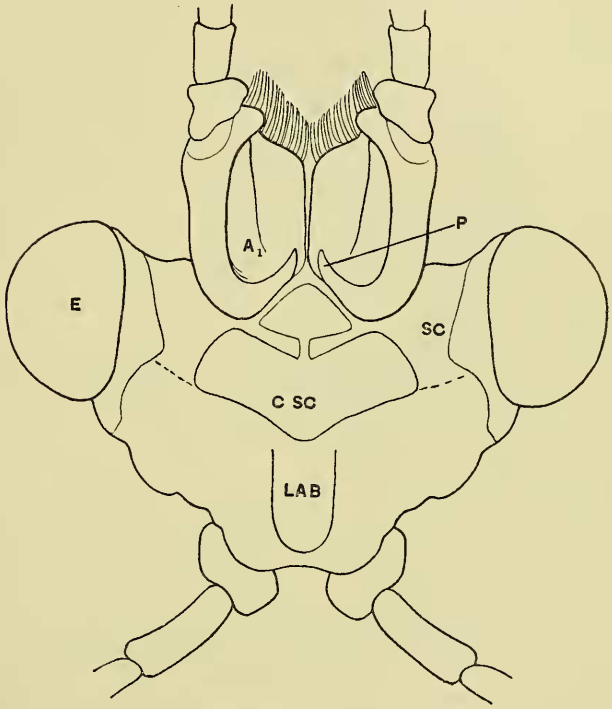
The cardo and stipes are not free like the four joints of the palpus, but are attached by their inner surfaces to the sides of the haustellum. Maxillary lobes not shown.

For the sake of convenience it is easy to divide the mouth-parts of adult Trichoptera roughly into those with a very elongate haustellum*, and with no mandibles or with the mandibles much reduced, and those with a shorter haustellum and a pair of powerful well-developed mandibles. In the former case, for example in *Phryganea* and *Limnophilus*, the cardo of the first maxilla is articulated to the head in a small angle or niche formed at the point where the gena curves down as the triangular flap (text-fig. 3, F). In these genera, both cardo and stipes are elongate and lie along each side of the stalk or peduncle of the haustellum and carry off the maxillary palpi at their distal end some distance away from the head. In the latter case, for

* Haustellum was the name given by Lucas (19) to what he regarded as an enormously developed fleshy labium projecting from the head as a sort of proboscis by means of which caddis-flies obtain their nourishment. In reality the haustellum is a modification of the region of the hypopharynx.

example in *Rhyacophila*, the cardo and stipes are much shorter, so that the maxillary palpi are carried close to the head instead of at a distance from it. In such cases the angle or niche in which the cardo is articulated is much larger, and in this angle the cardo is attached to the head by the whole of its inner surface, whereas in *Phryganea* and others this angle or

Text-figure 4.



Sericostoma personatum.

Head from in front with the palpi and lobes of the first maxillæ dissected off (diagrammatic). × 36.

E. Eye. A_1. First segment of the antenna, excavated to receive tips of the palpi. *P.* Upturned process. *LAB.* Labrum. *SC.* Soft chitin. *CSC.* Clypeal sclerite.

niche receives only the proximal end of the cardo, which is provided with a stout condyle for the attachment of a powerful muscle arising from the tentorium. The stipes is carried at right angles to the cardo, so that the general direction of the palpi is dorsal. The female of *Sericostoma personatum* agrees

with this general description; but in the male the angle or niche has developed into a deep somewhat rectangular excavation of the gena, which is carried right back as far as the lower part of the eye and the subocular wart. Above it is bounded by the lower margin of the clypeus. The whole of this area (text-fig. 2) is reserved for the cardo and stipes which are very closely attached along their inner surfaces. The stipes has been forced back close to the head and back upon the cardo, both cardo and stipes being almost vertical in direction (text-fig. 2, ST & C). The stipes is a long sclerite, narrow at the base, broadening out gradually towards the distal end, where the palpus is inserted. It apparently gives only the slightest support to the maxillary lobe, as the stipes always comes away from the latter in dissection with great ease, and the chitinous bar, which in other Trichoptera the stipes sends in as a supporting connection with it, cannot be discovered. The cardo is much reduced, being visible at the side as a narrow chitinous splint.

Thus the two maxillary palpi completely cover the clypeus and front of the head, and their chitinous, convex, outer surfaces form a kind of mask or false front, beneath which the chitin of the clypeus has become thin and in places delicate and transparent (text-fig. 4, SC).

The labrum is fairly large, with a knob or enlarged basal piece. The mandibles, though present, are very much atrophied, but may be detected in a careful preparation one on either side of the base of the labrum, as a pair of thin pointed splint-like pieces of chitin. In most other Trichoptera well-developed mandibles are commonly found.

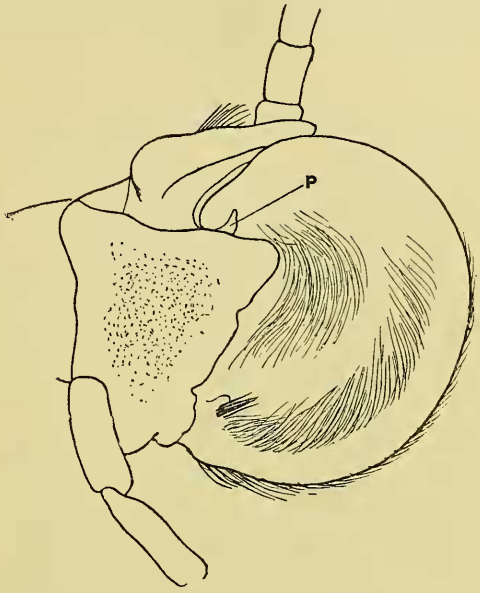
The basal joint of the antenna requires further description. Text-fig. 5 is a sagittal section of the head and gives a view of the relations between the maxillary palpus and the antenna. Text-fig. 4 gives a view from in front after both the palpi and lobes have been removed.

From an inspection of these figures it should be clear that these enlarged basal joints meet each other behind, but are excavated in front on their inner surfaces to receive the tips of the ascending maxillary palpi. The inner front part of each basal antennal joint is scalloped out into a slot into which the palpus tip is neatly fitted and locked by means of the little upturned process (text-figs. 4 & 5). The tip of the palpus also is modified to serve this end, as is mentioned and illustrated further on (see p. 468, Section iv.).

In addition to the mask or false front to the head formed by the palpi there is also a false top to the head formed by these two greatly enlarged basal segments of the antennæ, which extend backwards nearly as far as the occiput, covering nearly the whole of the top of the head. The whip-like remainder of the antenna springs, as if from the head itself, from the extreme anterior corner of this large basal segment. Each basal segment on the inner excavated side is white in colour and composed of

two "windows" of thin delicate chitin divided by a median bar of thicker chitin running dorso-ventrally. The segment itself is almost immobile, but its enlarged size allows for the presence of muscles by which the long whip-like remainder of the antenna can be moved.

Text-figure 5.



Sericostoma personatum, ♂.

Sagittal section of the head, with the palpus of the first maxilla and the first joint of the antenna seen from the inside (diagrammatic). × 27.

The shape of the tentorium appears to indicate limited antennary movements, as the two columnar endosternites or supporting pillars, which run from the cross-bar at the occipital foramen across the inside of the head to the clypeus, are simple, without wings or lateral expansions from which, when present in *Phryganea* and other genera, arise numerous powerful muscles to the antennæ. In the female of *S. personatum*, where the antennæ have much smaller basal segments, the tentorium is, however, similar to the tentorium of the male in the absence of its wings.

The head of the female is more or less normal. The maxillary palpi are fairly long 5-jointed appendages; the chitin of the clypeus is dark brown in colour and of equal thickness to that of the rest of the head. The mandibles are also much longer,

being visible under a strong power without the need of special microscopic preparation. The first segment of the antenna, though much larger than the succeeding segments, is separated from the first segment of the other antenna by a wide space, and bears no sort of resemblance to the eccentric form of these segments in the male. The cardo is also much larger than the cardo in the male, and instead of being practically vertical beside the vertical stipes it is at right angles to the latter. The stipes is shorter and broader than the same piece in the male, and the palpi are so hinged upon it as to point outwards and away from the head.

iv. The Scent Organs of *Sericostoma personatum*.

More detailed examination of a detached palpus of a male reveals the following additional facts.

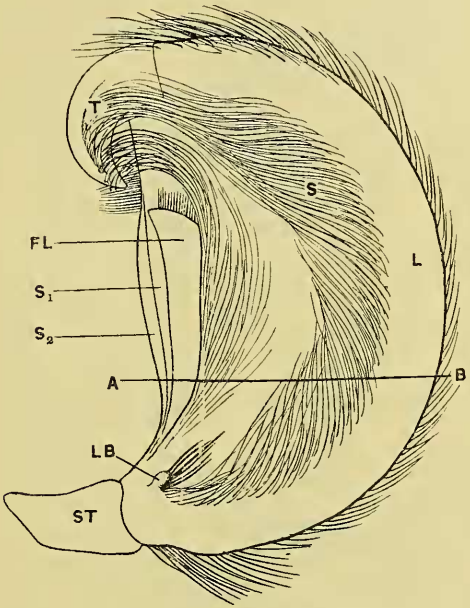
The deep brown, comparatively thick chitin of the convex outer side ceases abruptly in a transverse line towards the tip so as to leave the soft white tip of the palpus (composed of thinner chitin of a lighter colour) to fit more easily into the base of the antenna. On the inner surface at the base is a small lobe with two or three short black bristles at its base (text-fig. 6). These bristles in cross-section are seen to be fluted.

In side view the outer margin is very convex, the inner margin, which is applied to the head, more or less straight. The outer surface is very convex, and the inner surface applied to the inner surface of its fellow is concave. But the concavity is full of very long silky hairs, which curve up and around in a semicircle to protrude near the tip into the hollow in the base of the antennæ. In the figures only a few of these hairs are sketched in. This huge hair-tuft is bounded on the outside by a rather pronounced lip, bare except for a row, on the margin, of small black bristles, in cross-section seen to be fluted (text-fig. 7, FH), and on the inside by a flap (text-fig. 6, FL), which projects and keeps the hairs tucked in so that they are prevented from straying in an untidy mass on both sides. Further reference to this flap is given below. It runs down towards the base of the palpus, where it is continuous with the "lip" of the convex outer margin. Higher up it carries a fringe of hairs much shorter and stouter than the silky hairs of the scent-gland tuft. The ends of these hairs are somewhat swollen. The flap ends abruptly higher up so as to leave a channel between it on one side and the lip of the palpus opposite on the other side. Between these two promontories the long hairs sweep out beyond the edge of the palpus, and are sometimes visible as "fluff" projecting from between the two basal antennal segments behind.

Under the flap is the opening into a large sac which occupies the whole of the interior of the palpus from the top to its extreme bottom near the stipes.

Beneath this sac is another sac which opens by a longitudinal slit along the inner margin of the palpus beneath the opening of the first sac. At first I thought this sac was only an artefact, imagining that the membrane lining the hard chitinous convex surface of the palpi had come away. But sections showed the existence of a distinct cellular lining to the inside of this chitin, and there can be no doubt that the sac in fact exists.

Text-figure 6.



Sericostoma personatum, ♂.

Palpus of the first maxilla, seen from the inside with most of the silky hairs removed (diagrammatic). × 39.

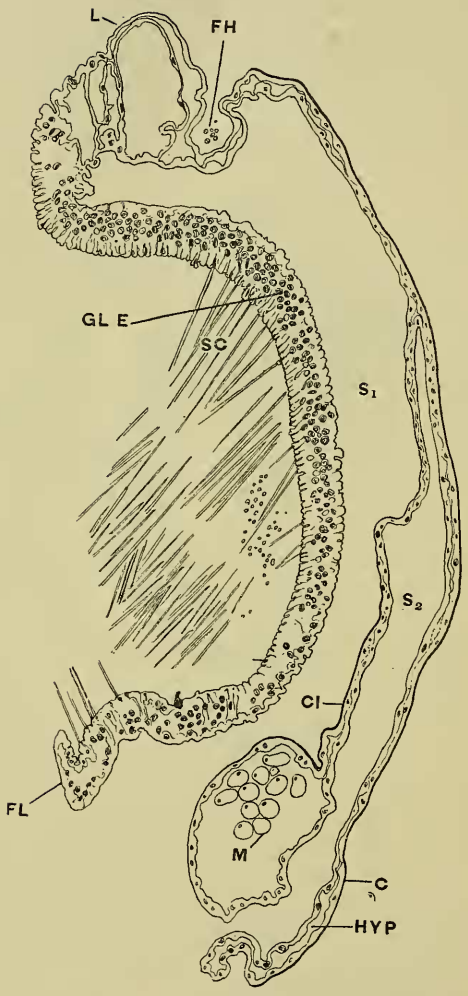
ST. Stipes. *L.* Lip. *LB.* Lobe. *FL.* Flap. S_1. Entrance to sac 1. S_2. Entrance to sac 2. *S.* Scent hairs. *T.* Tip of palpus.

A study of transverse sections of the palpus affords us the following histological information.

Text-fig. 7 is through the line AB in text-fig. 6. It shows the two sacs and the septum between them, and the layer of large, deeply stained, glandular cells at the base of the silky hairs.

The hypodermis beneath the outer, convex cuticle of the palpus is composed of a double layer of flat squamous cells. The septum between the two sacs is formed by the innermost cell-

Text-figure 7.



Sericostoma personatum, ♂.

Transverse section along the line AB in text-fig. 6. Length of section 1·1 mm.

S_1. Sac 1. S_2. Sac 2. *FL.* The Flap. *L.* Lip. *FH.* Fluted hairs. *GL.E.* Glandular epithelium. *C.* Cuticle. *HYP.* Hypodermis. *SC.* Scent hairs. *CI.* Chitinous intima. *M.* Muscle-fibres.

layer which runs up to encircle a number of muscle-fibres. This septum is stiffened by a comparatively thick chitinous intima (text-fig. 7, CI), which runs in from the entrance to cover about half of the outside wall of the inner sac.

In the sections, the "lip" (L) has been accentuated owing to the sinking in of the tissues beneath it to form a hollow where the fluted edges of the sections of the dark hairs are seen. Under this lip the two squamous layers of cells are widely separated the one from the other and the space between them traversed by strands. The cells are also larger.

On working round to the inner surface of the palpus one finds the concavity full of an immense thickness of hairs seen to be circular in cross-section and containing a central canal of small bore. The cuticle supporting these hairs is produced into elongate papillæ containing the alveoli in which the scent hairs are fixed. Beneath the cuticle the hypodermis consists of a glandular epithelium of elongate cells, specialised formative cells called by Graber trichogens, in which the scent is secreted [(**10**) p. 188]. On account of the fact of the immense number of these cells and of the hairs which they support, it has not been easy, from an inspection of sections of unfixed material, to say definitely whether there is a single trichogen cell to each hair or whether there are several (text-fig. 8). Usually in the scent organs of the Lepidoptera there is one cell—one hair; but Bertkau (**20**), in the case of the Noctuine genera *Hadena* and *Dichronia*, points out that there is not one giant cell to each of the hairs of the scent tuft (which are of enormous length), but several smaller cells belong to each hair.

That these hairs may act as scent organs it is necessary for them to remain in connection with the living hypodermic tissue.

Text-fig. 8 shows how a pore-canal or channel runs up to the base of each alveolus through the chitinous papilla, thus putting into communication the cutaneous appendage with the hypodermic trichogen cell.

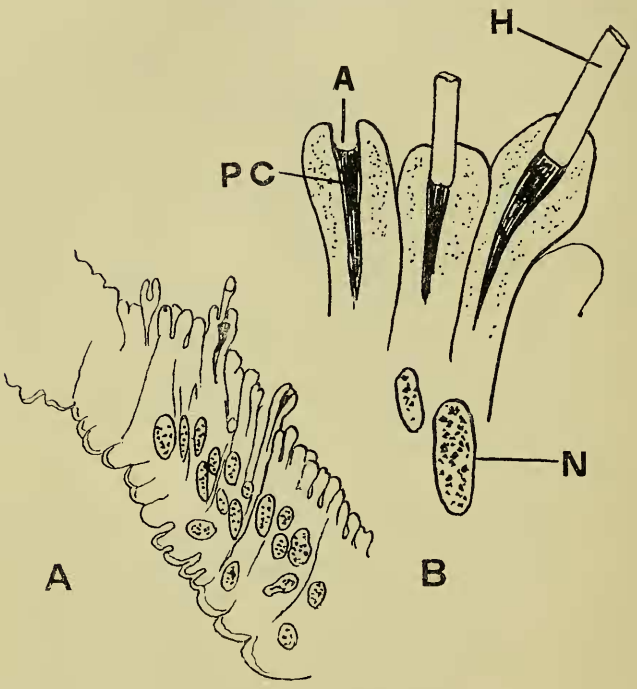
No opening pores were found either at the base of or at the tip of the hairs, and probably the scent secretion runs up the canal within the hairs by capillary attraction and becomes diffused by osmosis into the outer air. In the androconia and scent hairs of the Lepidoptera it is now generally held [Berlese (**12**) p. 533] that the secretion reaches the air by osmosis, as apertures in the integumentary appendages are no longer thought to exist.

The cuticle of the inner surface is plicate and the hypodermic cells are much smaller. Strands of tissue run across between the hypodermis of the inner and outer layers, being very clearly seen where the two layers of cells diverge from each other in the "lip."

It will be remembered that Müller (*supra*, p. 460, Section i) describes the male during mating as separating the maxillary palpi and spreading out the hair around the head "wie ein Heiligen-

schein." As a result of my study of these palpi, no very clear or concise expression of the manner in which this is done can be offered. No longitudinal muscle-fibres as they occur, for example, at the base of scent hair-tufts in some Butterflies, were discovered attached to the bases of the hairs. A circular muscle around the hair within the alveolus, but at some point above the base, would serve to erect the hair. No such muscle has been detected.

Text-figure 8.



Sericostoma personatum.

A. Portion of the glandular epithelium, enlarged. Actual width varies from ·053 to ·03 of a millimetre.

B. Some trichogen cells very greatly enlarged.

Reichert objective $\frac{1}{12}$ homog. imm., with eyepiece No. 4 was used for the examination of the cells. The drawings are free-hand.

A. Alveolus. *H.* Hair. *PC.* Pore-canal. *N.* Nucleus.

It remains to consider the action of the stout muscle-fibres in the edge of the septum previously described. Their course is longitudinal from the base of the palpus to near the end. The result of their contraction would be to draw down the tip of the palpus and so make the convex outer margin still more convex,

in which event the long silky hairs, which are curved and so fit the normal amount of the convexity of the outer margin of the palpus, would slip out of their concavity over the "lip" of the outer convex edge and project as a "frill." This action is often suggested while manœuvring the detached palpus in the dissecting dish. Again, if we suppose that the palpi by the aid of their muscular attachments to the stipes can be easily divaricated the one from the other and their inner surfaces exposed, it seems probable that the natural resilience of the hairs in the live animal would account for their erection, as they are inserted at right angles to the surface on which they stand, but in repose are flattened down upon it because the two palpi are then held closely apposed to each other. Perhaps also in the live animal the natural elasticity of the inner surface of the palpus may result, when exposed as a free surface, in its becoming swollen and convex, rather than as in spirit-specimens, concave.

I do not think that the resemblance between the scent glands of Lepidoptera and those of Trichoptera can very profitably be carried into histological details. The papers on scent glands in Lepidoptera which I have consulted all show in one particular or another considerable differences from those of *Sericostoma personatum*, as, for example, in the presence of muscle-bands, in the arrangement of the trichogen cells, or the shape of the pore-canals and the position of the hair-tuft.

I have to thank Mr. Martin E. Mosely for kindly giving me the material for this study, Prof. Maxwell Lefroy for allowing me to work in the Laboratory at the Imperial College of Science and Technology, and Mr. E. Hargreaves for assistance in section cutting.

v. Literature.

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